

BREEDING SYSTEMS IN INDOMALESIAN SPINIFEX (PANICEAE: GRAMINEAE)

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SUMMARY

Coastal, psammophilous *Spinifex littoreus*, like other species of *Spinifex*, is dioecious in Indomalaysia, but exceptions to dioecism are found in West Java, the Molucca Islands, and occasionally in the Philippines and northern Borneo. There dioecism has become degraded on the female side to trimonoecism, and sporadically to typical andromonoecism, through restoration of male fertility in some or all flowers. Interpretations of an androdioecious breeding system for Malesian *S. littoreus* are unsustainable.

INTRODUCTION

Spinifex littoreus (Burm. f.) Merr. is a maritime, psammophilous, colony-forming grass with curved, rigid, pungent leaf-blades and conspicuous, globose, wind-dispersed infructescences. In some recent regional floras its sexual expression is described as dioecism: Blatter and McCann (1935) for Bengal, Bor (1960) for the Indian subcontinent, Gould (1994) for Ceylon, Henty (1969) for New Guinea, Hsu (1978) for Taiwan, Koyama (1987) for Japan; but other floras define the reproductive system as androdioecism: Gilliland (1971) for Malaysia, Lazarides (1980) for tropical Southeast Asia, Monod de Froideville (1968) for Java, and Telford (1993) for the Ashmore Reef, Timor Sea. The descriptions are usually complete for inflorescences, spikelets, and florets, which are well illustrated (Blatter & McCann, 1935; Gilliland, 1971; Hsu, 1978; Koyama, 1987; Telford, 1993). The descriptions are deficient for the flowers; no recent flora has the precise sexual portrayal of the 19th century illustrations in Labillardière (1804) and Buchanan (1880), or in Pilger (1904).

Androdioecism is emphasised for Malesia (Gilliland, 1971; Monod de Froideville, 1968; Van der Pijl, 1976, 1982). An androdioecious population would consist of interbreeding male and hermaphrodite plants (Cruden & Lloyd, 1995), but Charlesworth (1984) has concluded that every case of androdioecism of which she was aware was actually functional dioecism. Reported androdioecism in Malesian *Spinifex* "... needs to be carefully examined; judged from present evidence it seems improbable" (Connor, 1984); judged from the data to be presented here that conclusion was correct.

In this paper the sex forms of *S. littoreus* flowers are described, and the pollen fertility determined in some plants. The genetic structure of the population is deter-

mined and the distribution of sex forms is outlined. Orthodox dioecism prevails except in parts of the Philippines and Indonesia where genes restoring male fertility have arisen in female plants and appear to be advantageous.

Spinifex is an oligotypic, Old World, diploid ($2n = 18$) genus, three species of which are Australasian and the fourth, *S. littoreus*, is primarily Indomalaysian. Only in *S. littoreus* is there any departure from dioecism which characterises the subtribe Spinificinae of tribe Paniceae.

MATERIALS AND METHODS

Herbarium specimens on loan from BO, K, L, SING, and US, representing 106 gatherings, were used in determining sex forms.

Specimens seen are listed in the Appendix by country of origin, collector with number when available, sex form, and herbarium.

INFLORESCENCES, FLOWERS, AND FLOWERING

In *Spinifex* there is a conspicuous inflorescence dimorphism, one of the highly correlated characters in dioecious peregrinating grasses (Davidse, 1987; Quinn et al., 1994).

Male inflorescences 5–10 cm long, terminally and also at some upper culm nodes, are many single, rigid, erect, spike-like racemes in spatheate, umbel-like clusters. Sharply bristle-tipped racemes have 5–10 deciduous, alternate, spikelets of two, similar, awnless florets.

Female inflorescences up to 30 cm diameter, often solitary, are stellately globose, spatheate umbels of many coherent, single racemes each with a very long, scabrid, bristle-like rachis. One spikelet of two awnless florets is at the base of each rachis.

Male flowers comprise three anthers and two lodicules in each floret, and a rudimentary gynoeceum in the upper floret. Anthers are polliniferous, (4–)5–7 mm long, shortly tailed, on broadly liguliform filaments 10 mm long; lodicules are c. 1 mm long.

Female florets are dissimilar. Of the two florets the lower and smaller may be neuter or have three sterile anthers and sometimes a gynoeceum; the upper, larger, lodiculate floret comprises three sterile, filamented anthers, and a gynoeceum of a beaked ovary 1 mm long or more, styles about 6 mm long usually fused below but separate above, and plumose stigmas 7–10–14 mm long. Lodicules are almost 1.5 mm long and longer than those in male plants, a dimorphism noted for *Spinifex* by Pilger (1904). Anthers in female flowers are 0.7–1.2–1.5 mm long, flared at the base, white, pollenless, and on liguliform filaments about as long as the palea. Caryopses are c. 3.5 mm long.

In western Java, on the Moluccan Islands, and in the Philippines globose inflorescences that are structurally female in appearance and have spikelets with female florets, may also produce spikelets with both hermaphrodite and male florets. Here a two-flowered spikelet has:

- 1) lower floret male with three polliniferous anthers 4–5.25 mm long, on liguliform filaments \geq palea; lodicules are c. 1 mm long; there is no gynoecium; this floret is rarely neuter;
- 2) upper floret hermaphrodite with three polliniferous anthers 4–5.5 mm long on filaments as long and wide in the male flower and \geq palea; lodicules are c. 1 mm long; stigmas are 8–11 mm long on styles 4–7 mm usually split to the ovary beak. Caryopses are c. 3.5 mm.

These two florets conform to andromonoecism (Cruden & Lloyd, 1995) in a panicoid spikelet. As well, there are two-flowered spikelets with the typical female flower syndrome – lower floret neuter or with three sterile anthers, and the upper floret with a gynoecium and three male sterile anthers. Together these two kinds of spikelets constitute a trimonoecious inflorescence (Cruden & Lloyd, 1995). The frequencies of each kind of spikelet in an inflorescence were not determined. In two inflorescences I found only andromonoecious spikelets.

Sizes of floral organs in all sex forms are in Table 1.

Pollen stainability was determined in four of the trimonoecious plants; the range was large, from 6% stainable in *Lamb A/85*, 31% in *La Rivière* (1920), 87% in *Beguin 927*, and 95% in *Santos 8264*. Stainable pollen was present in anthers of both upper and lower florets of a spikelet.

Stigmas and styles, and anther filaments are contorted or twisted in anthoecia before emergence; they are clearly fully formed and mature, and unfold to emerge. Anthesis in male florets seems limited; the paleas and lemmas do not appear to become widely separated and anthers emerge at the apex of the anthoecium.

Table 1. Mean floral organ sizes in two species of *Spinifex*.

	Anther length (mm)	Style length (mm)	Stigma length (mm)	Ovary length (mm)	Lodicule length (mm)
<i>S. littoreus</i>					
Male *	5.51 \pm 0.08	–	–	–	0.98 \pm 0.05
Female *	1.15 \pm 0.03	5.87 \pm 0.12	10.03 \pm 0.39	1.1 \pm 0.04	1.44 \pm 0.08
Male †	4.65 \pm 0.10	–	–	–	1.15
Hermaphrodite †	4.83 \pm 0.10	3.4	9.2	1.0	0.96
Female ‡	1.28 \pm 0.06	4.5	9.16	0.87	1.1
<i>S. longifolius</i>					
Male *	3.93 \pm 0.48	–	–	–	0.8
Female *	0.87 \pm 0.03	4.14 \pm 0.55	7.0 \pm 1.56	1.0	1.3

* In dioecious plants.

† In andromonoecious spikelets.

‡ In female spikelets of trimonoecious inflorescences.

In female florets, which though markedly lodiculate do not open, stigmas are exerted at the apex of the enclosing anthoecium for perhaps 10–14 mm, and the small sterile anthers are exerted perhaps for 1 mm, or reach as far as the apex of the anthoecium often remaining entrapped in stigmas.

In hermaphrodite florets, where the paleas and lemmas do not separate, the three large polliniferous anthers emerge at the apex of the anthoecium together with the stigmas. In an andromonoecious spikelet it can be safely assumed that the larger upper floret of a spikelet is first to flower. There is no suggestion of protogyny in hermaphrodite flowers though there is every reason to suspect it; stigma and anther emergence in the upper floret precedes anther emergence in the lower floret, creating an interfloral dichogamy with two separate releases of pollen from one spikelet (Connor, 1987).

All specimens of *S. longifolius* R. Br. collected on the Australian coasts of the Arafura and Timor Seas are clearly dioecious. No departures were seen among 40 sheets from BRI. Floral organs are generally smaller than in *S. littoreus* (Table 1).

GEOGRAPHIC DISTRIBUTION OF SEX FORMS

A general outline of the distribution of sex forms is in Figure 1; details are in the Appendix or from appropriate regional floras.

Spinifex littoreus is the only member of the genus in the Northern Hemisphere, and at its north-western limits, India on the Arabian Sea, in Ceylon and on the Coromandel Coast of India, all specimens are strictly dioecious. From Burma and Thailand male and female plants had been gathered. In coastal Cambodia and Vietnam specimens were male and female. On the south-eastern Chinese coast and on Hainan

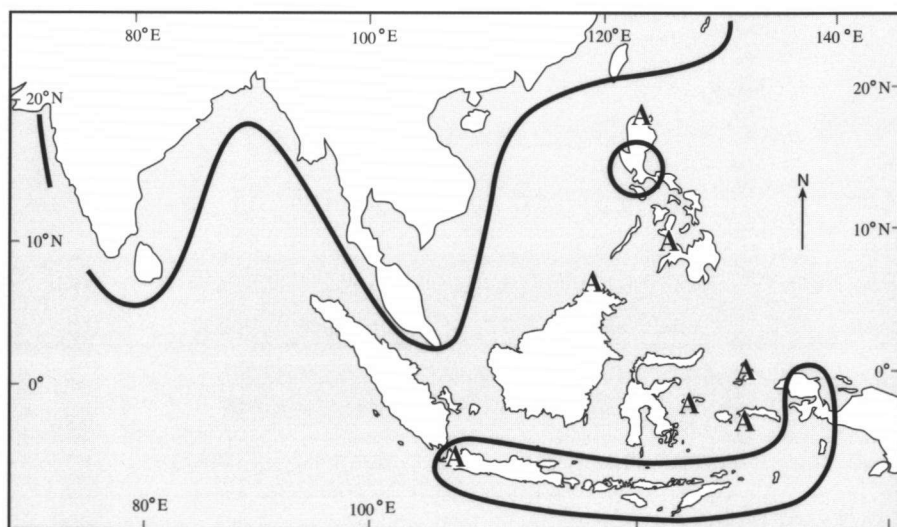


Fig. 1. Distribution of sex forms of *Spinifex littoreus*; male and female plants on coastal sandy beaches included by solid lines. A = andromonoecious spikelets present.

Table 2. Distribution and frequencies of sex forms of *Spinifex littoreus* in Malasia (from herbarium specimens). M = male; F = female; MH = andromonoecious; F,MH = trimonoecious. Geographic units after Van Steenis-Kruseman (1950).

Region	Sex form			
	M	F	MH	F, MH
<i>Java (and neighbouring islands)</i>				
West Java	2	1	•	4
Central Java	3	•	•	•
East Java	2	3	•	•
Kangean Archipelago	4	3		
Madoera	1	1	•	•
<i>Lesser Sunda Islands</i>				
Bali	1	1	•	•
Lombok	2	•	•	•
Soembawa	1	•	•	•
Komodo	•	1	•	•
P. Roti	1	•	•	•
East Timor	1	•	•	•
<i>Molucca Islands</i>				
Halmaheira	•	•	•	2
Ternate	•	•	•	1
Sula Is.	•	•	•	1
Ambon	•	•	1	•
<i>Borneo</i>				
Balampagan	•	•	•	1
<i>Philippines</i>				
Mindoro	2	1	•	•
Babuyan Is.	•	•	1	•
Luzon	6	2	•	•
Negros	•	•	•	1
<i>New Guinea</i>	1	1	•	•

Island male and female gatherings are represented, but on Taiwan the few collections I saw were from male plants. Specimens from the Ryukyu Islands, at the northern limit of distribution, are both male and female. No departures from strict dioecism were seen among 45 sheets examined – some sheets bore both sex forms (Appendix).

For Malasian distributions the geographic units in 'Flora Malesiana', Series I, Volume 1 (Van Steenis-Kruseman, 1950), although smaller than those used for the surrounding continental and insular areas, allow for the greater detail necessary to indicate areas of sex form variation.

Veritable male and female plants are present in collections from the central and southern Malay Peninsula, and from Java, the Lesser Sunda Islands, and the Philippines (Table 2; Appendix).

In West Java, the central Molucca Islands, and on Balampagan Is., northern Borneo, and in the Philippines, plants with inflorescences of female structure may be trimonoecious (Table 2). Two specimens, *Ramlanto 412*, Ambon, Moluccas, and *Santos 7782*, Magsaysay Island, northern Philippines, had spikelets of male (below) and hermaphrodite (above) florets; spikelets of female flowers were lacking so far as I could see, and those inflorescences are classified as simple andromonoecism.

The salient areas for trimonoecism in apparently female inflorescences are West Java and the Molucca Islands (Table 2). In the Moluccas all apparently female inflorescences bear pollen-fertile anthers. I doubt that these data reflect chance collections; they must indicate, because of their consistency, the reproductive habit of *S. littoreus* in the Moluccan Islands. Males, the most easily and frequently collected sex form, are not represented in the Moluccan gatherings though present in West Java where trimonoecism is at a relatively high frequency. The structure of the male inflorescence is unaffected there.

The absence in herbaria of either male or female specimens from a particular locality should not be simply interpreted as 'male/female not present', though a collecting note on *Santos 7782*, "♀ only", may mean that it was the only sex form on that beach. This specimen, significantly, seemed completely andromonoecious – one of two such specimens seen (Table 2; Appendix).

DISCUSSION

Sex forms

Plants of *S. littoreus* from West Java correctly led Monod de Froideville (1968) to the conclusion that this taxon is not always strictly dioecious. Plants with spikelets of hermaphrodite and male flowers in female-like inflorescences were interpreted as if they were exclusively hermaphrodite, and the breeding system, therefore, the rarely successful androdioecious syndrome. Just what specimens influenced Gilliland (1971) towards androdioecism is uncertain, because every specimen that I have seen from the Malay Peninsula is unequivocally male or female (Appendix).

Only in Malesia is there any departure from the strict dioecism seen in most of Indomalesia. In Java, the Moluccas, and sporadically in the Philippines and northern Borneo, there are plants with the hermaphrodite and male flowers of andromonoecious spikelets in inflorescences otherwise with the construction for female flowers. Sometimes female spikelets are absent but this is less frequent than trimonoecism (Table 2). No Indomalesian specimens can allow *S. littoreus* to be described as androdioecious; most populations are dioecious. All other species of *Spinifex* are strictly dioecious with a primary sex ratio M/F = 1: *S. longifolius* of tropical and subtropical Australia (Connor & Jacobs, 1991, and Connor, *hic. comm.*); *S. hirsutus* Labill. of temperate Western Australia (Craig, 1984; Kirby, 1988); *S. sericeus* R. Br. of eastern Australia and northern New Zealand (Connor, 1984; Maze & Whalley, 1990) although Vickery (1975) referred to the sporadic occurrence of pollen fertile anthers in female florets in Australia.

Dioecism and dimorphic inflorescences are infrequent in the tribe Paniceae – three genera in 100, *Pseudochaetochloa* A. Hitchc., *Spinifex* and *Zygochloa* S.T. Blake –

and together constitute a notable tribal exception; panicoid dioecism is centred in Australia but its origins are unexplored; dioecism in *Spinifex* is unstable, or imperfect, only in eastern Malesia, a fact of significant evolutionary interest.

Evolution of andromonoecism

The opportunities for floral differentiation within and between spikelets in *Spinifex* are subject to the phylogenetic constraint of two florets in a panicoid spikelet. *Spinifex* has polliniferous anthers in the two florets of spikelets in a male plant, and in a female plant the spikelet has one pistillate floret. In one floret only, the lower floret in a female spikelet, is there an opportunity to increase sex form diversification. The andromonoecious spikelets with sexual elements in both florets have captured that opportunity and have, where adjacent female spikelets retained their customary sexuality in the upper floret, generated a trimonoecious inflorescence. Nowhere was a monoecious spikelet found, one that would comprise a lower male floret and an upper female flower, nor were two hermaphrodite florets in one spikelet – the ideal precursor to androdioecism – ever seen. Andromonoecism is a genetically less demanding alternative for a panicoid grass than monoecism.

I had outlined earlier the probable evolutionary pathway to dioecism in *Spinifex*, where dimorphic gender diversification is adopted rather than the monomorphic syndromes common to other members of the Paniceae (Connor, 1981, 1984). Chamaechory was incorporated there, but not the synaptospermous habit which could be beneficial because, potentially, caryopses of both sex forms would be dispersed together and could function as founders of a new population (Van der Pijl, 1982).

The favoured evolutionary pathway invoked both andromonoecism and monoecism at different times leading eventually to dioecism and to the prominent inflorescence dimorphism. Monoecism in *Spinifex* is limited to andromonoecism as a current reproductive state in *S. littoreus*. Andromonoecism is incorporated in a fully evolved, morphologically female inflorescence and not, as might have been expected, in male inflorescences. In a homozygous male sterile (female) spikelet that sexual redevelopment is essentially the restoration of male fertility so that the lower floret continues to lack a gynoecium, but the anthers are now polliniferous and anthers in the upper pistillate floret have also become polliniferous resulting in an hermaphrodite flower. No sex-linked male characters have accompanied the restoration of male fertility and the increase in maleness. The origin of andromonoecious spikelets in female inflorescences could be explained by invoking male fertility restorer genes entering the dioecious population and being selected. A male fertility restorer system is preferred over other possible mechanisms, e.g. an hermaphrodite mutant, but it may be difficult to detect a difference between restorer genes and a breakdown in the genetic system controlling male sterility. The exact maintenance of such a fertility restorer system is unclear, just as is the incomplete restoration of male fertility in some inflorescences. The system may only be in its infancy although in the Molucca Islands it seems firmly established.

As interpreted here, the breeding system seen in parts of Malesia is a secondary state derived from dioecism and not its antecedent. That conclusion has a parallel in the breakdown on the female side in *Datisca glomerata* (Presl) Baill. (Datiscaceae),

where females have become hermaphrodites; populations of interbreeding males and self-compatible hermaphrodites constitute androdioecism (Liston et al., 1990). Support for that origin of androdioecism in *D. glomerata* was indicated from chloroplast DNA studies (Rieseberg et al., 1992), but Swensen et al. (1994) using plastid *rbcL* results rejected that solution as inconclusive. The data on *S. littoreus* leave no room for doubt that the integrity of femaleness in a dioecious system has, in part, failed; that solution is more appropriate than one postulating a predioecious state still persisting at some localities.

Temporal and spatial differences between sex forms are present in *Spinifex*; male inflorescences emerge earlier than females throughout the geographic range of the genus (Connor, 1984). Spatial differences for sex form vary, but large colony sizes of individual plants (genets) are a constant feature. On the New Zealand coast one male colony of *S. sericeus* extended for c. 0.25 km along the dunes at Ahipara, and at Waipiro Bay there were only two large colonies along an extensive dune system, one male and the other female. A colony of a single sex form never occupies a dune system in New Zealand or Australia. Evidence of rapid colony formation by *S. littoreus*, both in time and space, is provided by Saulei (1988) for Papua New Guinea. Large colony size is seen by Lloyd (1982) as one character for which dioecism may be selective because dioecism would reduce the risks of autogamy in a large hermaphrodite colony. In *S. littoreus* it would seem that andromonoecious spikelets, either alone or mixed together with female flowers, have evolved to increase the chances of pollination and seed set that were reduced by the large spatial extent of single sex colonies and the overdispersal of male and female plants. One reason advanced as favourable for the evolution of dioecism could be responsible for its decline, but causality for the shift from dioecism to self-compatible andromonoecism requires the examination of natural populations and their ecological status especially in Indonesia.

CONCLUSIONS

Spinifex littoreus, a grass of sandy beaches in Indomalesia, is dioecious in its continental distribution; it is dioecious, too, at its northern limits on the subtropical Ryukyu Islands. On oceanic islands especially in the equatorial Molucca Islands and in West Java, spikelets with hermaphrodite and male flowers are also present in inflorescences of female morphology and sexuality, generating trimonoecism. When the female element of the dioecious system has degenerated, it has incorporated andromonoecism as a result of the invasion by genes for the restoration of male fertility, but only rarely is male fertility completely restored in an inflorescence. Male specimens seem infrequent, or even absent, where genes that produce andromonoecism have established. There is no evidence of the evolution of androdioecism in Malesia. No species of *Spinifex* has departed from dioecism except *S. littoreus*.

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APPENDIX

Specimens seen. Country of origin; Collector and number; Sex form (M = male; F = female; MH = andromonoecious; F, MH = trimonoecious) and Herbarium (between brackets).

CEYLON: Clayton 5211 M (US), 5896 M (US), 5979 F (K), 5980 M (K, US); Conamor 913 M (US, K); Davidse & Sumithraachchi 8826 M (US), 9102 M (US); Fosberg *et al.* 50990 M (K, US); Gould 13072 M (K), 13169 M&F (K); Looray M (K).

INDIA: Barber 1616 M (K); Janaki Ammal 791 M (US); Koelz 10884 F (K); Stoddart 1528 M (US), 1594 M (US); Thomson (1872) M (K); Venngopal & Jayaseelan RHT 21274 M (K), RHT 21274a F (K); Wight M (K).

BURMA and THAILAND: Kerr 4242a F (K); Marcan 2256 M (K); Parkinson 8810 F (K); Sanghachand & Smitinand 1120 F (K); Walker 7901 M (US).

CAMBODIA and VIETNAM: Clemens & Clemens 3057 M (US); A. S. Hitchcock 19415 M (US), 19416 M (US); Pierre M (US ex P).

SOUTHEASTERN CHINA (including Hong Kong and Macau): But 025 F (K); Chen Ping En 2337 M (US); Fung 20401 M (K); Lau 317 F (K); Shiu Ying Hu 6499 M (US), 12468 F (K); Taam 2096 M (US); Tate (1862) M (K); Vachell (1830) M (K).

TAIWAN: Henry (1926) M (US); Oldham (1864) M (K); Price 630 M (K).

RYUKYU ISLANDS: Fosberg 37116 M (K); Miyoshi Furuse 3303 F (K), 3481 M (K); Walker *et al.* 6949 F (K).

MALAY PENINSULA: Burkill 2263 M (K, SING), 3232 M (SING); Burkill & Md Haniff M & F (SING); Evans (1917) M (SING); Gwynne-Vaughan 366 F (L); Holtum 15168 M (SING); Kochummen M (SING); Mahmud Sider (1973) M&F (US); Md Shah 4058 & Sider M (SING); Ridley (1889) M (SING); Sinclair 7525 M (US); Sinclair & Kiah b. Salleh M (K, SING); Yapp 383 M (L).

JAVA: Backer 7754 F (L, BO), 15266 M (BO), 17883 M (BO), 20386 F (BO), 20763 M (BO), 24649 F (BO), 27172 M (L), 28089 F (L), 28699 M (BO), 29102 M (US), 29777 M (BO), 29815 F (BO); Buwalda 7170 M&F (BO, L); Kern 7782 M&F (BO), 8294 F, MH (BO); van Kregten 113 M (K); Murata *et al.* J 2085 F, MH (BO); La Rivière (1920) F, MH (L), La Rivière M (L); Scheffer (1871) F, MH (BO); van Slooten 2444 F (BO); Sun Hong-Fan 7701 M (BO).

LESSER SUNDA ISLANDS: Bloembergen 3081 M (BO, SING); Cinatti 192 M (L); Elbert (1909) M (BO); Meyer & Noerta 9073 M (BO); Saakov 4 F (BO); Sun Hong-Fan 9066 M (BO); Verheijen 2424 M (L).

BORNEO: Lamb A/85 F, MH (K).

PHILIPPINE ISLANDS: Clemens 44a M (US); M. S. Clemens (1915) M (US, BO); Escritor (1913) M (US); Loher 1757 M&F (K, US), 7235 F (K), M (BO); Merrill 419 M&F (K); Santos 7782 MH (L), 8264 F, MH (L); Sulit 5612 M (K, L, US).

MOLUCCA ISLANDS: Beguin 927 F, MH (L); Bloembergen 4640 F, MH (L); Nedi 263 F, MH (BO), 444 F, MH (BO, L); Ramlanto 412 MH (BO).

NEW GUINEA: Aët 320 F (BO, K); Buwalda 5560 M (SING).